

Evolutionary precursors of social norms in chimpanzees: a new approach

Claudia Rudolf von Rohr · Judith M. Burkart ·
Carel P. van Schaik

Received: 7 July 2010 / Accepted: 12 November 2010 / Published online: 20 November 2010
© Springer Science+Business Media B.V. 2010

Abstract Moral behaviour, based on social norms, is commonly regarded as a hallmark of humans. Hitherto, humans are perceived to be the only species possessing social norms and to engage in moral behaviour. There is anecdotal evidence suggesting their presence in chimpanzees, but systematic studies are lacking. Here, we examine the evolution of human social norms and their underlying psychological mechanisms. For this, we distinguish between conventions, cultural social norms and universal social norms. We aim at exploring whether chimpanzees possess evolutionary precursors of universal social norms seen in humans. Chimpanzees exhibit important preconditions for their presence and enforcement: tolerant societies, well-developed social-cognitive skills and empathetic competence. Here, we develop a theoretical framework for recognizing different functional levels of social norms and distinguish them from mere statistical behavioural regularities. Quasi social norms are found where animals behave functionally moral without having moral emotions. In proto social norms, moral emotions might be present but cannot be collectivized due to the absence of a uniquely human psychological trait, i.e. shared intentionality. Human social norms, whether they are universal or cultural, involve moral emotions and are collectivized. We will discuss behaviours in chimpanzees that represent potential evolutionary precursors of human universal social norms, with special focus on social interactions involving infants. We argue that chimpanzee infants occupy a special status within their communities and

C. Rudolf von Rohr (✉) · J. M. Burkart · C. P. van Schaik
Anthropological Institute & Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich,
Switzerland
e-mail: claudiarvr@aim.uzh.ch

C. Rudolf von Rohr
University Research Priority Program in Ethics, University of Zurich, Zollikerstrasse 117,
8008 Zurich, Switzerland

propose that tolerance towards them might represent a proto social norm. Finally, we discuss possible ways to test this theoretical framework.

Keywords Chimpanzees · Social behaviour · Evolution of social norms · Evolution of moral behaviour

Introduction

Recent genetic studies suggest that the hominin lineage and the one giving rise to chimpanzees split as recently as 6–7 million years ago (Glazko and Nei 2003; Goodman et al. 1998; Ruvolo 1997, for a review). In evolutionary terms, this is a short period of time. Consequently, humans and chimpanzees share numerous similarities in terms of both cognition and behaviour (Boesch 2007; de Waal 2005; Tomasello and Call 1997). Chimpanzees manufacture and use tools (Goodall 1986). They exhibit significant cultural variation between communities (Whiten et al. 1999) and show a remarkably rich social life (de Waal 1982). They hunt cooperatively (Boesch 1994), share food and, like humans, engage in inter-group killings (Wrangham 1999). Recent findings also confirm that chimpanzees possess simple elements of a theory of mind (Call 2007; Call and Tomasello 2008).

Taken together, these findings have led many to wonder whether there are any uniquely human characters left. One possibility is that our capacity to engage in moral behaviour (besides religion and art) is what makes us different from our closest living relatives. Therefore, several researchers recently began to investigate possible building blocks of human moral behaviour in chimpanzees such as consolation, instrumental helping and prosocial behaviour in food-related contexts. They could show that chimpanzees console, i.e. initiate affiliative contacts with recipients of aggression and that such behaviour reduces recipients' postconflict stress levels (Fraser and Aureli 2008; Fraser et al. 2008; but see Koski and Sterck 2007, 2009b). Furthermore, chimpanzees help human experimenters and other conspecifics upon request to reach their goals (Warneken and Tomasello 2006; Yamamoto et al. 2009) and occasionally also do so even spontaneously (Warneken et al. 2007). However, studies that tested chimpanzees' tendencies to behave prosocially in food-delivering experiments have so far yielded only negative results (Jensen et al. 2006; Silk et al. 2005; Vonk et al. 2008; Yamamoto and Tanaka 2010).

In sum, most of the existing studies exploring possible building blocks of human moral behaviour in chimpanzees have capitalized on their tendencies and capacities to behave prosocially in different contexts. Here, we focus on another element of human moral behaviour, i.e. on social norms, specifically on those related to harm. We recognize that the question of what exactly moral behaviour is or what it comprises leads to difficult and quite controversial ethical as well as meta-ethical discussions. However, there seems to be consensus that social norms, especially those dealing with harm, constitute an important element of moral behaviour (Bernard 2008). Here, we explore in a comprehensive way whether evolutionary precursors of such norms are present in our closest living relatives, the chimpanzees. Our approach consists in focusing on the existence of bystander reactions upon

potential norm violations. By focusing on *uninvolved* bystanders, rather than on direct victims of potential norm violations, we are able to exclude that reactions to norm violations are simple responses to the violation of individual interests but rather are based on more generalized expectations about “how one ought to behave” (Fehr and Fischbacher 2004). Thus, we use *uninvolved* bystanders as a critical test case.

Many terms we employ are commonly used in the empirically oriented moral-psychological as well as -sociological literature. We are aware of the complex philosophical debate on some of these terms. However, since a thorough philosophical explanation of them is beyond the scope of this paper, we apply commonly used definitions for the purpose of this paper.

Human social norms

Human morality comprises a spectrum of complex phenomena, ranging from moral emotions and moral behaviour to moral reasoning, moral judgment and to abstract concepts of right and wrong (Greene and Haidt 2002). Yet, in our daily lives morality comes almost naturally to us. We don't jump the queue and we help the elderly or handicapped. In other words, we *behave* morally and do so often without previous deliberate consideration of the pros and cons of such behaviour. Generally, human moral behaviour reflects a set of particular values and principles, both of which are often embedded in social norms. Social norms are such an integral part of our social life (Jasso 2001; Sober and Wilson 1998) that we are often completely unaware of their omnipresence and our automatic adherence to them (Young 2002). These norms shape our family life (Bott 2003) as well as our relations with friends, the opposite sex (Kanazawa and Still 2001; Scott 2000) and even with strangers. They regulate politics (Axelrod 1986; Khagram et al. 2002), the economy (Platteau 2000), and even what we wear and eat. Their social function includes the promotion of cooperation (Axelrod 1986) and social order (Elster 1989) and the smoothening of social interactions in general.

To make things more complicated, social norms can be explicit or implicit. In the former case, they are either written down or spoken about openly, but in the latter, they are not openly stated and maybe not even consciously represented. This raises an important problem. How can outsiders know what is considered a norm within a certain society? In humans, this problem is easily solvable provided we are able to speak the local language. We can simply ask people what they consider as appropriate or inappropriate behaviour in their society, and deduce the underlying social norms. But since our focus in this paper is on chimpanzees, a *nonverbal* species, we need to adopt another approach than language to find out which behaviours, if any, they might consider appropriate or inappropriate.

Social norms can be understood as behavioural regularities that are normative (i.e. entail a sense of oughtness in the moral sense) to a varying degree and generate *social* expectations (Hechter and Opp 2001; Horne 2001). We expect others to do or not to do certain things. These expectations do not have to be experienced consciously by the individual, but their satisfaction or violation might produce distinct reactions, thus making these expectations amenable to observation from the outside. Thus, when these expectations are fulfilled we expect to observe no, neutral or perhaps even

positive reactions such as friendly remarks or a smile. However, when a certain behaviour violates these expectations, then negative reactions almost always ensue (Hauser 2006). Notably, negative reactions are not only shown by the victims of a violation, the second parties (Fehr and Gächter 2002), but most importantly also by *uninvolved* bystanders, the third-parties (Fehr and Fischbacher 2004). *Uninvolved* bystanders can generally be defined as individuals who witness a norm violation and who have no particular relationship (i.e. kin or friendship) with the victim(s). While negative reactions from victims might simply reflect a reaction to the damage to individual interests, negative reactions from bystanders can be regarded as moral behaviour, since they provide no apparent benefits to the performers. Indeed, they may be costly in terms of emotional discomfort and risk of provoking retaliation (Horne 2001). Thus, the existence of negative reactions of bystanders towards specific behaviours allows us to draw inferences about the existence of social norms and moral behaviour on a *nonverbal* level. This is not to say that all social norms can be identified by means of negative reactions in bystanders. There might be social norms being present in the absence of such reactions. However, if negative reactions in bystanders do occur towards specific behaviours then we regard them as good evidence for the existence of social norms in a given social group, especially on a *nonverbal* level.

Negative reactions from bystanders may comprise bewilderment, anger or even indignation towards a violation. The fact that they associate different kinds of emotions with different kinds of violations (Hauser 2006; Nichols 2002, 2004; Turiel 2005) exemplifies the above-mentioned degree to which a behavioural regularity is normative. For example, a violation of the behavioural regularity not to talk aloud in a silent train compartment tends to be associated with relatively flat emotional responses like angry looks or grumbling whereas a violation of the behavioural regularity not to maltreat a child is highly emotionally charged and elicits vehement emotional reactions such as indignation. Thus, behavioural regularities of the former that are associated with relatively cool emotional responses are sometimes referred to as *conventions* rather than *norms* (Bicchieri 2006). However, there may be various gradations and levels of emotional response to violations that make it inevitably difficult to make a precise distinction between conventions and norms (Young 2008). In the following, we elaborate this distinction more in detail for we need to specify what we will be looking for in chimpanzees (see Table 1).

Conventions

Conventions can be characterized by arbitrary and therefore variable contents. Furthermore, they are relative to social systems which means that they vary geographically as well as temporally between and even within different societies (Turiel 1983). In other words, they are culturally based and therefore their innate basis is limited. Additional examples of conventions are the mode I use to greet people or how I address them. Although conventions are only weakly normative and conformity is more requested¹ than compulsive, we prefer to conform to them since

¹ However, there might be conventions for which conformity is not only requested but rather compulsive due to possible severe consequences upon their violation (e.g. which side of the road to drive on).

Table 1 Human social norms can take the form of conventions, cultural social norms and universal social norms

	Conventions	Cultural social norms	Universal social norms
Content	<i>Variable</i>	<i>Variable</i>	<i>Invariable, harm-related</i>
Arbitrariness	<i>Yes</i>	<i>Yes</i>	<i>No</i>
Variation in space and time	<i>High</i>	<i>High</i>	<i>Low</i>
Cultural basis	<i>Yes</i>	<i>Yes</i>	<i>Limited</i>
Innate basis	<i>Limited</i>	<i>Limited</i>	<i>Yes</i>
Normativeness (<i>in the moral sense</i>)	<i>Low</i>	<i>High</i>	<i>High</i>
Conformity	<i>Requested</i>	<i>Compulsive</i>	<i>Compulsive</i>
Intensity of emotional reaction upon violation	<i>Low</i>	<i>High</i>	<i>High</i>
Emotional reaction is empathy-driven	<i>Not necessarily</i>	<i>Not necessarily</i>	<i>Yes</i>
Presence in chimpanzees	<i>Controversial</i>	<i>Unlikely</i>	<i>Anecdotal</i>

There is currently controversy over whether chimpanzees' cultural variants in behaviour constitute conventions as found in humans. Chimpanzees are unlikely to exhibit cultural social norms but might exhibit social norms related to harm, which might constitute species universals

we are endowed with a strong tendency to conform to what everyone else around us does (Richerson and Boyd 2005) and because it feels good to conform (Christensen et al. 2004).

Chimpanzees are well known for their cultural variants in different behaviour patterns, including tool use, grooming or courtship (Whiten et al. 1999). Such behaviours spread within a community through social learning (Whiten 1998; Whiten et al. 1996) and individuals are more likely to adopt them as they become more common within a group (Whiten et al. 2005). Some researchers suggest that chimpanzees, like humans, might even conform to such cultural behavioural variants (Whiten 2010; Whiten et al. 2005). However, evidence for conformity in chimpanzees is still weak and future studies in this area will have to show that the animals are not simply copying what has been demonstrated most but rather that the animals exhibit a disproportionate tendency to copy what the majority does (Efferson et al. 2008). Furthermore, some researchers argue that some of the behavioural variants in chimpanzees might constitute conventions. Especially, specific grooming and courtship behaviours that in themselves are completely arbitrary and whose meanings seem to be defined only by the individuals within a specific group are thought to represent conventions resembling those seen in human societies (Bonnie et al. 2007; Whiten 2005). The alternative explanation, however, could be that using them may simply be more efficient than using alternatives because their meaning is certain to be understood. Thus, chimpanzees might only groom in a specific way, i.e. adopt a specific posture, because this might be the most functional and efficient way to groom specific body parts of the grooming partner, given their behaviour, and thus grooming partners might coordinate their activities

to achieve this physical end rather than a social one (i.e. follow a specific convention). In short, their behaviours might simply reflect responses to physical affordances that, as a by-product, lead to uniformity. Tool using techniques most likely follow this principle. They are characterized by a functional and goal-directed task and constitute efficient means to achieve physical ends; for example, termites must be extracted from their mound to be eaten. Thus, chimpanzees most certainly do not use specific tools because everybody else does so, although this might be the case for an individual's first use of a tool, but because after some experience they understand the utility and effectiveness of the practice (Bonnie et al. 2007; Turiel 1983). Whether specific cultural behavioural variants really constitute conventions or whether they are best described as *statistical* behavioural regularities, will be discussed later in this paper (see section “[How to distinguish between statistical behavioural regularities and different evolutionary precursors of human social norms?](#)”).

Cultural social norms

In humans, the repertoire of cultural variants in behaviour patterns seems to be infinite thanks to our highly elaborated capacity for cumulative culture (Richerson and Boyd 2005; Tomasello 1999). Importantly, humans often assign to such cultural behavioural regularities a strong normative component and hence conformity to them is often compulsory. An extreme example of this kind is veiling, which may be associated with strong emotional reactions when women fail to conform (Moghadam 2003). We classify such behavioural regularities as *cultural social norms*. Since they are, like conventions, culturally based, their content is also highly arbitrary and therefore variable and varies in space and time (Murdock 1967). However, we will leave aside this kind of social norms for we expect them to be absent beyond the human species (Boyd and Richerson 1987) because they are often used to signal ethnic (as well as religious) group affiliation and loyalty (Hill et al. 2009).

Universal social norms

Although the content of cultural social norms differs considerably between groups, it seems that all cultures share a capacity to appreciate harm-related violations (Abarbanell and Hauser 2010; Killen et al. 2002; Nucci 2001). Importantly, this capacity seems to emerge early in ontogeny (Nucci and Turiel 1978; Smetana 1981, 2006; Smetana and Braeges 1990). Given these two facts, it seems plausible and most parsimonious to assume that norms against harm might constitute a species *universal*. Furthermore, the fact that harmful behaviour generates strong emotional responses (Nichols 2002) indicates, in turn, that norms prohibiting harmful behaviour are perceived as highly normative and consequently imply compulsive conformity. Importantly, the strong emotional reactions towards harm-related violations largely emanate from our capacity to empathize with the harmed victim whereas the emotional reactions towards the violation of a convention or a cultural

social norm are not necessarily empathy-driven but rather emanate from the fact that “someone failed to behave properly”.

Unsurprisingly, chimpanzees, like other nonhuman primates, are also reported to strongly react towards harmful behaviour in their midst, especially when it might seriously endanger the social fabric and/or relationships (de Waal 1991, 1996; Flack and de Waal 2002; Goodall 1986; Killen and de Waal 2000). Despite the anecdotal evidence suggesting the presence of norms related to harm in chimpanzees, systematic studies are still lacking. To date, humans are still widely perceived to be the only species on this planet to possess social norms and to engage in moral behaviour (Hill 2009; Hill et al. 2009)—this probably due to a view centred on cultural social norms. Here, we question this assumption anew by focusing on a particular category of social norms, namely those related to harm and their possible prehuman precursors in chimpanzees.

Chimpanzees

Chimpanzees live in large multimale–multifemale communities. At all times, adult males are dominant over adult females (Goodall 1986). Despite the fact that dominance is highly formalized among males and between the sexes, chimpanzee societies are nevertheless characterised by high levels of mutual tolerance, as reflected by the presence of extensive social learning and hence behavioural and material culture in this species (van Schaik 2003; Whiten et al. 1999). Furthermore, being subordinate in a chimpanzee society does not necessarily imply having no control over dominants as is the case in highly despotic species such as rhesus monkeys (*Macaca mulatta*) (de Waal 1989). For instance, subordinate male chimpanzees are reported to form coalitions against dominant males, sometimes causing dramatic changes in the dominance hierarchy (de Waal 1982; Nishida 1983; Nishida and Hosaka 1996) and female chimpanzees to engage in protective, potentially violent coalitions against male aggression (Baker and Smuts 1994; de Waal 1996; Newton-Fisher 2006).

Humans share additional similarities with chimpanzees (and various other nonhuman primates). The slow growth of chimpanzees (Boesch 2009) necessitates a long period of childhood in which socialization plays a crucial role in the acquisition of adequate adult behaviour (Goodall 1986; Goodall et al. 1979). Chimpanzees also form long-term stable relationships (i.e. friendships) which are characterized by mutually supportive and affiliative behaviour (Boesch and Boesch-Achermann 2000; Reynolds 2005). They have also developed strategies that help them to resolve issues between them; they engage in conflict management. Soon after conflicts, former opponents come together and engage in peaceful post-conflict interactions (i.e. reconciliations) (de Waal 2000). Their function is to curtail damage to valuable relationships and to restore them by means of friendly behaviour (Cords and Aureli 2000). Alternatively, when there is no valuable relationship at stake, such behaviours may generally indicate the end of hostility and signal that the actor’s intentions are peaceful again, thereby facilitating non-aggressive interactions between former adversaries (Silk 2000). In sum, chimpanzees’ high mutual

tolerance, the presence of subordinate leverage over dominants, their slow life history and sophisticated social behaviour can all be considered important preconditions for the presence of evolutionary precursors of universal social norms in this species.

The various cognitive abilities of chimpanzees constitute a further important precondition in this respect. Although there is a lively debate about chimpanzee cognition (Call and Tomasello 2008; Penn and Povinelli 2007; Povinelli and Vonk 2003), recent evidence confirms they possess a rudimentary theory of mind (Call and Tomasello 2008, for a review). Importantly, they are able to regulate their immediate behavioural drives and act against them. Recent evidence from several delay-of-gratification, exchange and temporal discounting tasks indicates that chimpanzees are able to exhibit patience and to suppress immediate impulses that would lead to immediate benefits to acquire more valuable future rewards (Beran and Evans 2006; Dufour et al. 2007; Osvath and Osvath 2008; Rosati et al. 2007).

Finally, and most importantly, chimpanzees show empathetic competence. Although it is still too early to draw any firm conclusion about chimpanzees' capacity to understand emotions in others, experimental research done by Parr (2001) and Parr and Hopkins (2000) suggests that chimpanzees obtain emotional information from conspecifics most likely by sharing the other's emotions. Chimpanzees responded to emotional video stimuli with negative valence with decreased skin temperature and increased tympanic temperature. In humans, these physiological responses correlate with negative emotional arousal (Bauer 1998; Wittling 1995). Furthermore, chimpanzees seem to possess some basic understanding of the emotional meaning of facial expressions of conspecifics. In a matching-to-meaning task they were able to match video stimuli that conveyed an emotional meaning to the corresponding facial expressions (Parr 2001). Chimpanzees, like humans, exhibit contagious yawning (Anderson et al. 2004; Campbell et al. 2009), which in humans is based on the capacity to empathize (Lehmann 1979; Platek et al. 2003). Supposedly, the ability to recognize oneself in the mirror is also related to empathy (Bischof-Köhler 1989). Chimpanzees pass the mirror self-recognition test exhibiting self-other distinction (Gallup 1970; Kitchen et al. 1996) and thus are thought to possess initial stages of self-awareness (Gallup 1979).

Koski and Sterck (2009a) paralleled chimpanzee cognitive processing and their ability to understand other's emotional states with a developmental classification of the same capacities found in human children and propose that chimpanzees exhibit empathetic competences that operates at the level of *quasi-egocentric empathy*, possibly reaching initial stages of *veridical empathy*. The authors suggest that if chimpanzees operate on the *quasi-egocentric* level of empathy they would, in an appropriate experimental paradigm, no longer display mere emotional contagion when confronted with a distressed conspecific but would instead be able to regulate their own distress to some extent due to improved regulatory control. Furthermore, they would be able to show initial other-regard. However, their response to the other's need would reflect what would be appropriate for them in the same situation, regardless whether it would satisfy the other's need. For example, children, performing on this level of empathy, are reported to bring their own favourite toys

to comfort their crying friends instead of the friends' favourite toy (Hoffman 1979, 2000).

Only on the level of *veridical empathy* a complete separation of self and other's distress is achieved, enabling an appropriate response to the other's specific needs (Zahn-Waxler et al. 1992). As mentioned above, chimpanzees help other conspecifics and human experimenters in instrumental-helping tasks to reach their goals that they cannot reach themselves if showing overt signs of needs (Warneken et al. 2007; Warneken and Tomasello 2006; Yamamoto et al. 2009). Koski and Sterck (2009a) suggest that such instrumental helping might indirectly support that chimpanzees empathize on the *veridical* level of empathy. However, the authors also emphasize that chimpanzees' helping behaviour in these experiments might not stem from a representation of the other's emotional state but simply from an understanding of the other's goal and the underlying motivation to reach it. Taken together, these findings indicate that chimpanzees possess elaborate social expertise and cognitive skills, both of which are rarely seen in the animal kingdom. However, they are not yet sufficient as evidence for a capacity to engage in moral behaviour.

To establish whether evolutionary precursors of moral behaviour in chimpanzees occur, we have to investigate whether they, like humans, react to norm violations as *uninvolved* bystanders. We will argue that an essential precondition for the evolution of social norms is the existence of "personal norms", representing the *personal* expectations of how an individual wants to be treated, because it seems implausible that one would form expectations about how others should be treated before forming expectations about how oneself wants to be treated. Evidence of such "personal norms" in chimpanzees is ample and discussed below.

"Personal norms" and potential evolutionary precursors of universal social norms in chimpanzees

Experiments and observations show that chimpanzees express their frustration, i.e. protest, when their *personal* expectations are violated. For example, chimpanzees respond negatively in a token-exchange task when they observe how a conspecific obtains a more preferred reward for the same token. Thereupon, chimpanzees frequently refuse to complete exchange interactions with the experimenter (Brosnan 2006; Brosnan et al. 2005). Furthermore, there is experimental evidence that chimpanzees "punish" conspecifics that steal their food by pulling a rope that causes the food platform to collapse and the food to fall out of the thief's reach (Jensen et al. 2007). This experiment supports anecdotal observations that chimpanzees treat food, including highly valued food such as meat, with remarkable "respect for ownership" (Goodall 1971; Mitani 2009) and hence possibly expect others not to steal it. Chimpanzees also protest when they do not receive support from their coalition partners in agonistic encounters (de Waal 1982, 1996), when they have no access to a preferred grooming partner, when grooming is not provided or when they become the victim of aggression for no apparent reason thereby serving as scapegoats for dominants (own observations). These protests may take the form of temper tantrums, which involve hysterical ear-piercing screaming, hitting the ground or body and chasing off the "offender" (Brosnan 2006; de Waal

1996), and are comparable to those seen in young children (Potegal 2000). However, moral behaviour starts where such *personal* expectations are generalized and extended to others and therefore become *social* expectations. In sum, previous work has largely focused on the existence of *personal* expectations in chimpanzees in order to show their sense of social regularity. Our approach differs from previous work primarily in its attention to the existence of *social* expectations in this species, i.e. expectations about how other individuals should behave among themselves, and to explore them *experimentally*. So far, there is only anecdotal and observational evidence of chimpanzee bystander reactions, which might be indicative of the existence of *social* expectations and hence possible candidates of evolutionary precursors of social norms in the context of harming others. In the following, we will discuss this line of evidence.

Preventing social disruption

In chimpanzees, high-ranking males often show policing behaviour (i.e. third-party interventions). Such interventions function to break up aggressive encounters between group members and often are impartial or even on behalf of the victim (Boehm 1994; de Waal 1982, 1984; de Waal and van Hooft 1981; Goodall 1986). Captive female chimpanzees are reported to regularly mediate between former opponents, thereby facilitating grooming between them and hence reconciliation (de Waal 1982; de Waal and van Roosmalen 1979), but also to intervene in ongoing conflicts between other females (de Waal 1982; de Waal and Hoekstra 1980). Functionally, policing behaviour is thought to control conflicts (Flack et al. 2005; Frank 2003), to help group members to build up larger and more diverse social networks (Flack et al. 2006), and in the case of high-ranking males, to assert their social as well as sexual interests (Castles and Whiten 1998; de Waal 1984). Proximately, however, third-party interventions might express what de Waal (1996) called a basic “*community concern*”. Thus, chimpanzees seem to be able not just to care about their own relationships but also about the relationships of others in their community (de Waal 1996). However, the exact motivations underlying the above-mentioned behaviours may be diverse and difficult to disentangle. For example, an alternative explanation for policing behaviour might be that interveners are just annoyed by the disturbance and take action to put a stop to it (Goodall 1986).

Controlling escalating male violence

Chimpanzee males regularly engage in noisy charging displays to show off their physical strength. In the majority of cases, group members, after making sure not being located within reach of the rowdy males, just ignore such outbreaks. However, occasionally male charging displays become violent and may even lead to injuries (de Waal 1996; Goodall 1986; Muller 2002). Other chimpanzees are reported to react to such escalating outbreaks with great excitement, which can include “waa” barking. Such vocalisations are loud and sharp sounds typically emitted by bystanders and are interpreted as protests, indicating “sympathy” for the victim, and seem to occur only in dramatically escalated situations (de Waal 1996; Goodall

1986; Killen and de Waal 2000; Köhler 1925). Furthermore, female chimpanzees in the wild as well as in captivity sometimes form coalitions against too aggressive males, which eventually force them to stop their harassment (de Waal 1982, 1996; Newton-Fisher 2006).

All these examples of third-party behaviours, including policing, mediation, protest vocalisation and protective coalitions, are likely to go psychologically beyond pure egoism in that they involve at least some degree of prosocial motivation. However, one could still argue that individuals that perform such behaviours follow their individual interests. In the following, we will argue that the strongest indication that bystanders intervene out of a prosocial motivation involves attacks on infants. Compared to adults, chimpanzee infants occupy a special status within their groups and thus are objects of special treatment. We therefore hypothesize that severe aggression against infants could constitute a violation of a social norm prescribing adequate treatment of infants.

Tolerance towards infants

Throughout the primate order, including humans, newborns and infants elicit a high degree of attraction (Alley 1980; Blaffer Hrdy 1999; Hrdy 2005; Lorenz 1943). Accordingly, positive social interactions with infants constitute a common behavioural pattern in these species. In chimpanzees, the same attraction can be observed. They are very curious about every new member in their community and want to satisfy their curiosity by examining the baby closely. Depending on the mother's individual characteristics, her social status and her mothering experience, she will allow other group members to come close and to watch the baby intently. In captivity, and probably also in the wild, it can be observed that adults, knowing about the protective nature of mothers, respect the intimacy between the mother and her newborn by keeping their distance, but nevertheless attentively watching the pair. However, infants and juveniles, with their impetuous behaviour, will take every opportunity to try to sneak a peek of the newborn or to touch it. This often provokes hostility or restrictive behaviour from the mother. However, they will soon have learned their lesson and adjust their behaviour towards the baby and its mother and will sit quietly next to the mother by simply observing her and her newborn (Hess 1997). It seems that from childhood on (but also later) chimpanzees learn that infants in their midst are objects of special treatment by learning to recognize the contingencies between their own behaviour towards the infant and the reaction of the mother and to behave in a way that does not provoke negative reactions from the mother (de Waal 1991). First contacts between group members and the newborn occur on average 6 weeks after the infant's birth and are characterized by gentle touches, sniffing and grooming. As the infants grow older, at the age of around 6 months, other group members are also allowed to hold them and play with them (van Lawick-Goodall 1968). This even includes adult males (see Fig. 1). Chimpanzees exhibit towards infants in their midst an extreme tolerance afforded to no other age-sex class. Infants are allowed to climb over adults, to jump on their shoulders, to steal their food or tools and even to interfere during mating. Furthermore, it is not uncommon to observe adult males share their food with

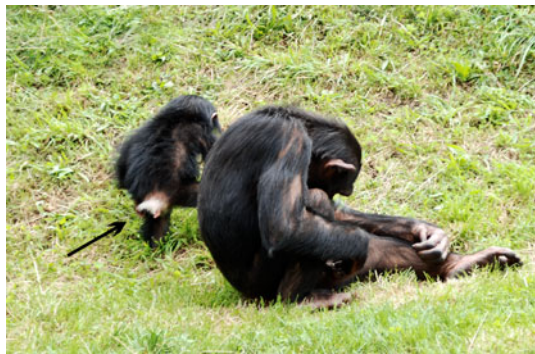
Fig. 1 An adult male chimpanzee plays with a 6 months old infant. The infant shows a typical play face with laughter



infants that sit next to them while they are eating (Bennett 1996, cited in Reynolds 2005; de Waal 1982; Goodall 1971, 1986; Hirata and Celli 2003; Inoue-Nakamura and Matsuzawa 1997). In sum, infants are above the law.

Body size and proportions, vocal and motor behaviour, as well as distinctive infantile characteristics such as bright faces, protruding foreheads, large eyes and their typical white tail tufts (see Fig. 2) make a chimpanzee infant a special stimulus. Generally, these stimulus dimensions are argued to elicit care, attention and protection as well as to inhibit aggressive behaviour in mothers and especially in other group members (Alley 1980, for a review). Interestingly, the white tail tuft of chimpanzee infants becomes conspicuous exactly at the time, with 6 months, when infants leave their mothers and start to get into contact with other group members, sometimes annoying them as we have seen (van Lawick-Goodall 1968). Such contacts often lead to play bouts including tickling and wrestling between infants and other group members and are characterized by the same tolerance as mentioned above. Several researchers suggested that chimpanzees self-handicap during play with younger play mates seemingly adjusting their behaviour to the still limited capacities of the younger partner (Goodall 1986; Hayaki 1985; Mendoza-Granados and Sommer 1995). Flack et al. (2004) could actually show that chimpanzees do take into account the other's capacities and do exercise self-handicapping by lowering their play intensity the greater the age difference between

Fig. 2 Six months old infant with white tail tuft (*black arrow*)



them and their play partner. Furthermore, it seems that older play partners increase their play signalling during play bouts that occurred in proximity to the mothers, especially young ones, to emphasize that the interaction between them is friendly and intervention or punishment is not necessary (Flack and de Waal 2002; Jeannotte 1996).

Despite the almost unlimited tolerance infants normally enjoy, it may happen that they become victims of aggression. Such highly dramatic incidents provide us with valuable insights into the nature of chimpanzees' expectation of how to treat infants. De Waal (1982) reports an anecdote in which a 3 year old infant happened to stay in the way of a highly aroused bluffing male and was picked up and swung against a wall by him. Bluffing adult males sometimes lose all of their social inhibitions and may regard any object as good enough to underscore their impressive displays (de Waal 1996; Goodall 1971). Interestingly, this incident provoked massive vocal protests ("waa" barking) from several adult females. Goodall (1971) reports a similar anecdote from the wild in which an old male approached the victimized infant, picked him up and took care of it until his mother could finally join her infant.

Aggression towards infants can also have lethal consequences as in the case of infanticide. So far, there is evidence of about 35 observed or inferred infanticides including inter- as well as intra-community killings from 7 different chimpanzee communities that have been observed for more than 2 decades (Murray et al. 2007; see also Townsend 2007). Since chimpanzees are a highly territorial species and engage in coalitional killing of neighbours (Wrangham 1999), infanticide between communities is not as puzzling as intra-community infanticide, which is in virtually all cases performed by non-kin of both sexes (Goodall 1977; Townsend 2007). Generally, the adaptive significance of infanticide is still poorly understood because of its rarity and variability (Hiraiwa-Hasegawa and Hasegawa 1994; Murray et al. 2007). However, chimpanzee infanticidal behaviour is very selective since not every infant in a group faces the same risk of being killed (Hamai et al. 1992). Murray et al. (2007) report that within the Kasekale community of Gombe, 112 newborns were counted between 1964 and 2005 and yet only 5 of these infants became victims of intra-community infanticide. This suggests that chimpanzees do not kill infants out of a general aggressiveness towards them (van Schaik 2000).

But how can the presence of an evolutionary precursor of a social norm not to harm infants be reconciled with the occurrence of intra-community infanticide performed by non-kin in chimpanzee communities? In the same way as in humans: Social norms reflect the interest of society (e.g. a trustworthy social environment), which may be at odds with those of particular individuals (e.g. paternity certainty). The fact that bad things happen does not imply that social norms against them do not exist. On the contrary, social norms exist *because* bad things happen. We must not forget that natural selection favours individuals that are highly adaptable in their behaviour and thus will show strategic and tactic behavioural responses towards external as well as internal circumstances (Fuentes 1999; Sommer 2000). Especially nonhuman primates exhibit such complexity in their behaviour (Fuentes 1999) and chimpanzees, like humans, are most pronounced in this regard (Boesch 2009; Wrangham et al. 1994). Thus, behaviours such as tolerance towards infants

and severe aggression against them are not mutually exclusive behavioural strategies but—depending on specific individual and/or socio-ecological circumstances—alternative strategies in nonhuman primates (Blaffer Hrdy 1979; van Schaik 2000), as well as in humans (Bethea 1999; Daly and Wilson 1988; Gilbert et al. 2009; Hatters Friedman and Resnick 2007). In other words, infanticide is not an all-or-none phenomenon but may or may not occur under the appropriate conditions (van Schaik 2000). Tolerance of infants is therefore most probably a matter of degree. In the case of male-led infanticide, tolerance of infants may decrease as the male's paternity becomes more and more uncertain. This in turn increases the risk of lethal aggression towards a female's infant (van Schaik et al. 2004). In chimpanzees (as well as in other animals), infants that are likely to be sired by stranger males may therefore face the highest risk of lethal aggression (Hamai et al. 1992; Hiraiwa-Hasegawa and Hasegawa 1994; Kawanaka 1981; Nishida and Kawanaka 1985; Norikoshi 1982; Takahata 1985). In the case of female-led infanticide, tolerance of other females' infants may decrease as the competition between females for resources increases (Townsend 2007), as they compete for good foraging areas which may be limited (Pusey et al. 1997).

There is no need to discuss here any further the various proposed adaptive or non-adaptive explanations for infanticide in chimpanzees in detail. Instead, we concentrate on what is most important for our hypothesis, namely the anecdotal evidence of bystander reactions towards such incidents. Researchers that happened to witness infanticide report massive reactions from male as well as female bystanders, including vocal protests such as “waa” barking, persistent screaming, highly aroused individuals and even risky behaviour such as interventions and/or coalitionary defence of the mother-infant pair (Goodall 1977; Hamai et al. 1992; Murray et al. 2007; Sakamaki et al. 2001; Townsend 2007). However, the problem with such incidents is that they not only occur infrequently but also unexpectedly and are highly chaotic by nature. This makes it very difficult for observers to keep track of every single individual and to report its distinct reactions. Only more systematic evidence of bystander reactions in the context of severe aggression against infants will allow us to distinguish whether such behaviours are indeed the result of a violation of an expectation about how to treat infants or whether there are alternative explanations for such behaviours. Furthermore, we have to show that completely *uninvolved* bystanders react towards severe aggression against infants, for this would constitute the most unequivocal evidence for the existence of *social* expectations of how to treat infants in chimpanzees. This is only achieved with the help of well-controlled experiments, as we will detail below.

In what follows, we first propose a preliminary theoretical framework that allows us to decide whether a specific behavioural regularity observed in chimpanzees is merely *statistical*, or whether it might qualify as an evolutionary precursor of a social norm, *as such*, and hence might have the function to prescribe behaviour. Then, we propose a preliminary gradient from quasi social norms to collective social norms, drawing on the example of appropriate social interactions with infants. For that, we assume that specific psychological mechanisms that evoke tolerance and inhibit aggressiveness towards infants constitute an important biological foundation upon which humans, with their elaborate cognitive capacities, ultimately

developed institutionalized norms that prescribe appropriate behaviour towards infants. This means that in modern, large-scale societies this social norm became explicitly formulated in ethical as well as in legal codes and that perpetrators are officially prosecuted, condemned and sent to prison. Finally, we will discuss possible experiments in chimpanzees to test our framework.

How to distinguish between *statistical* behavioural regularities and different evolutionary precursors of human social norms?

Examples abound of chimpanzee behaviours that may be of interest to others in their group. Chimpanzees occasionally share food with each other and regularly groom each other. Males regularly hunt and patrol the boundaries of their territory and chimpanzee females everywhere are very caring mothers. These behaviours are acquired under strong genetic influences or largely through social learning, or some combination.

However, so far, there seem to be no reports of bystander reactions when individuals fail to comply with such behavioural regularities. Therefore, we propose to categorize behavioural patterns that regularly occur in a social group but upon violation provoke no bystander reactions as *statistical* behavioural regularities. We clearly separate them from those behavioural regularities that, upon violation, provoke reactions from bystanders and as such might constitute an evolutionary precursor of a social norm, *as such*. As shown above, there are situations in which chimpanzees are sensitive to how other group members behave and thus do react to such incidents. Therefore, as discussed above, the occurrence and nature of bystander reactions towards an individual that shows deviant behaviour constitute a crucial feature to distinguish behavioural regularities that are merely *statistical* from such that might be “*normative*”. Table 2 illustrates this distinction and a preliminary gradient from quasi social norms to collective social norms such as humans do have them.

Throughout the primate order (and well beyond it), we can observe the regularly occurring behavioural pattern of generalized tolerance towards infants. This tolerance together with an inhibition of aggression is largely conditioned by a genetic disposition and mediated through the summed stimulus value of specific infantile characteristics. In contrast to violating a mere *statistical* behavioural regularity, a serious violation of tolerance towards infants almost invariably produces vehement reactions from bystanders as we have seen. Here, we examine in more detail how such reactions might be explained, and offer three possible interpretations, from purely mechanistic to fully moral.

(1) *Quasi social norm*: It might be that bystander reactions are simply caused by specific cues such as the persistent high-pitched screams emitted by the victimized infant or by the frenzied screams emitted by its mother, the combination of both or by any other cues. Since there is an inherent emotional linkage between the individuals of a social group (Preston and de Waal 2002) the distress of the infant and that of its mother easily spreads to other animals in the group. Although bystander reactions that are simply triggered by specific cues may appear moral to the outside observer, they are not. These reactions are only moral from a functional

Table 2 Key features indicative of the presence of social norms (and their precursors), *as such*, rather than in a mere *statistical* sense

	<i>Statistical</i> behavioural regularity	(1) Quasi social norm	(2) Proto social norm	(3) Collective social norm
Behavioural regularity	e.g. Food-sharing, grooming, hunting, etc.	e.g. Generalized tolerance towards infants	e.g. Generalized tolerance towards infants	e.g. Generalized tolerance towards infants
Bystander reactions upon violation	Absent	Present (<i>elicited by specific cues</i>)	Present (<i>elicited by empathetic competence</i>)	Present (<i>elicited by enhanced empathetic & cognitive capacities</i>)
Moral emotion (e.g. indignation)	Absent	Absent	Present (<i>individualistic</i>)	Present (<i>individualistic & collective via shared intentionality</i>)
Third-party punishment ^a	Absent	Present (via <i>simple rule</i>)	Present (via <i>indignation</i>)	Present (via <i>indignation</i>)
Social institutions (norm- maintaining)	Absent	Absent	Absent	Present (via <i>shared intentionality</i>)

A preliminary gradient from quasi social norms to collective social norms is proposed

^a Variable feature that might depend on individual as well as social factors (e.g. willingness to punish, risk of retaliation, social structure, social complexity)

perspective, hence the term *quasi social norm*. Furthermore, individuals that are observed to attack the perpetrator during such incidents might only follow a simple strategy (e.g. Marsh 2002) such as “when an infant screams blue murder, then attack (if hierarchically possible) the individual that is closest to it”. In short, they only follow a simple strategy that is activated under specific social circumstances and adhere to it no matter what initially caused the infant’s screaming.

Since incidents with a high intensity of aggressive arousal have a strong social facilitative effect in nonhuman primates (Hall 1964) other group members are immediately brought on to the scene harassing the perpetrator. Such a scenario might be erroneously interpreted as a collective effort to “punish” the perpetrator. Bystander reactions that can be best explained this way probably do not reflect violated *social* expectations about the appropriate behaviour towards infants and hence most likely do also not involve emotions comparable to indignation on the part of the bystander towards the perpetrator. Thus, bystanders in this category probably do not possess any specific inference on how the distress of an infant and the behaviour of a perpetrator are linked together and thus are not able to perceive harming infants as a norm violation per se. Note, however, that this interpretation relies on assuming the existence of some automatic reactions, such as the emotional linkage among group members and thus strong social facilitation of aggression. These assumptions need not be parsimonious.

(2) *Proto social norm*: If bystander reactions cannot be explained by simple stimulus–response mechanisms, then it might be that bystanders respond to the

specific context namely that “an individual harms an infant”. In short, they respond to the norm violation per se. In this case, bystander reactions most likely reflect violated *social* expectations, and therefore their reactions might also involve emotions comparable to indignation in humans, which in our species is often the driving force to punish wrongdoers. The step from a *quasi social norm* to a *proto social norm* whose violation per se produces distinct reactions from bystanders most likely necessitates the capacity to exhibit some empathetic competence, because this would enable bystanders to understand the mistreated infant’s and its mother’s distress to some extent and also its cause. To date, it seems that apes but probably not monkeys exhibit empathetic competence because monkeys seem to lack the capacity to attribute mental states to others (Cheney and Seyfarth 1990; Povinelli et al. 1991; Tomasello and Call 1997). Accordingly, macaque mothers fail to appreciate their infants’ distress after an aggression and display no concern for their infants’ need for comfort (Schino et al. 2004). As discussed above, chimpanzees are argued to be capable of some cognitive processing of others emotional states that exceeds mere emotional contagion (Koski and Sterck 2009a; Parr 2001). It therefore seems reasonable to argue that chimpanzees’ bystander reactions towards severe aggression against infants might stem from the perception of a norm violation per se rather than merely from the perception of specific cues or from a simple mirroring process of perceived distress in other group members. With some empathetic capacities in place individuals potentially also respond in more differentiated ways to situations in which an infant is screaming than when their responses are only stimulus driven because empathetic capacities probably enable individuals to draw more accurate inferences on what caused the infant’s misery. In other words, some empathetic competence enables individuals to recognize a social event as having a “moral” valence (Vetlesen 1994). Admittedly, it may be difficult to draw a clear distinction between a *quasi social norm* and a *proto social norm* since the development from one to the other is most likely a gradual one, since it includes empathetic (and thereby cognitive) capacities that themselves are argued to have emerged gradually during evolution (de Waal 2008; Preston and de Waal 2002).

(3) *Collective social norm*: Humans exhibit the same generalized tolerance towards infants as other animals. However, in addition to psychological mechanisms evoking tolerance towards infants, humans are also able to *reason* that infants are completely defenceless and therefore highly vulnerable creatures. To some of us infants also represent a symbol of innocence (Cross 2004). Additionally, our enhanced cognitive abilities enable us to imagine which impact (e.g. mental and behavioural disorders) maltreatment can have on the infant’s future life (Heim and Nemeroff 2001). Such elaborate concepts of infants certainly bolster our perception of infants as subjects of special treatment and certainly enhance our psychological mechanisms evoking tolerance and inhibition of aggression towards them. Furthermore, our ability to empathize at very complex levels, which is often referred to as cognitive empathy (Commons and Wolfson 2002; Hoffman 2000), enables us to represent fully and accurately the emotional state of a maltreated infant and that of its mother. In short, humans are endowed with advanced empathetic and cognitive abilities, which enable us to grasp the full extent and far-

reaching consequences of child abuse, which in turn increases our reaction of indignation towards child molesters.

Importantly, in humans indignation is not only communicated on a behavioural but also on a linguistic level. This means that with the advent of linguistic capacities, humans became able to communicate among each other about the deviant behaviour of others and articulate their indignation towards it, finally labelling deviant behaviours as something “wrong”. Perhaps the major consequence of language in the context of morality is that it can create a consensus among group members concerning a fully fledged moral system composed of abstract ethical concepts of right and wrong. The emergence of many uniquely human cognitive capacities including language and active teaching are tightly linked to and follow from shared intentionality, both phylogenetically and ontogenetically (Tomasello et al. 2005). It seems that this capacity not only plays a crucial role in how humans share information about their cultural world with each other but also how humans share emotions (which are argued to be relevant for moral behaviour) with each other. Shared intentionality is a suite of *cognitive* skills, i.e. the understanding of other’s psychological states, and of *motivational* skills, i.e. the strong desire to share them (Tomasello and Carpenter 2007).

Chimpanzees do to some extent understand the psychological states of their conspecifics as we have seen but they seem not to go beyond this in that they attempt to share them. Consequently, chimpanzees might experience “indignation” by the sight of severe aggression against infants in a fairly individualistic way since they are not able to form a “common psychological ground” (Tomasello and Carpenter 2007), namely a shared state of indignation towards harming infants. In analogy to shared intentionality, shared indignation goes beyond the simultaneous experience of indignation by different individuals but rather includes the awareness that “we collectively experience the same emotions to this specific social event”, which in turn can lead to collective protest and condemnation of the perpetrator. This exemplifies the collective character of a human social norm. It is this collectivity upon which the viability and the enforceability of a social norm ultimately rest on and which on current evidence appears to be absent in chimpanzees. Further below, we will resume the importance of shared intentionality and the collectivity enabled by it.

Third-party punishment is another feature of human social norms that deserve further discussion because it is considered to be a critical characteristic of human social norms (Fehr and Fischbacher 2002). As we have discussed earlier in this paper, except for the alpha male and on rare occasions also other group members, chimpanzees, unlike humans, do not readily impose punishment on those who transgress against others. There might be several reasons for that. First, as proposed for humans, the risk of retaliation might limit the extent to which chimpanzees punish transgressions against others. In chimpanzees, interference in an ongoing conflict can provoke retaliation from aggressors (Goodall 1971, 1986). Second, redirected aggression after an original conflict, known to occur in chimpanzees (Koski et al. 2007), might also limit the extent to which bystanders adopt a prominent role during and after conflicts. This especially might concern female bystanders whose physical strength is inferior to that of a male (Finch 1943), despite

the moderate sexual dimorphism in chimpanzees (Leigh and Shea 1995; Pusey et al. 2005). Third, although chimpanzees live in permanent social groups, they exhibit a fission–fusion social structure (Goodall 1986), which means that individuals of the same group spend their time alone in the forest or associate in subgroups which may vary in composition over hours and days (Reynolds 2005; Williams et al. 2002). Such a social structure might reduce the chance that bystanders, willing to punish, detect a possible norm violation.

The near-absence of third-party punishment in chimpanzees must be weighed against the evidence for humans. A recent cross-cultural study suggests that third-party punishment is not essential for norm enforcement. In small-scale societies of hunter-gatherers, second-party punishment seems to be sufficient to guarantee norm adherence (Marlowe 2009; Marlowe et al. 2008; but see Wiessner 2009). The authors argue that only in large and complex societies, characterized by an increased anonymity, does deviation from norms become more tempting and more difficult to monitor. Thus, third-party punishment is *not* a human universal and constitutes a trait that only becomes essential under specific conditions. In modern societies, third-party punishment therefore became formalized involving police, courts and prisons. Additionally, recent studies suggested that the fear of retaliation and its associated costs might limit the willingness of bystanders to punish (Denant-Boemont et al. 2007; Janssen and Bushman 2008). Thus, although the presence of third-party punishment in experiments serves to demonstrate the presence of specific social norms (Fehr and Fischbacher 2002), its absence does not automatically imply an absence of such social norms (or their precursors). Indeed, focusing exclusively on the explicit meting out of third-party punishment might result in overlooking more subtle behavioural patterns from which the presence of social norms (or their precursors) can also be inferred. Thus, the position of chimpanzees on the proposed continuum depicted in Table 2 remains undetermined.

Another way to guarantee the maintenance of social norms than through punishment is that individuals instruct, i.e. actively teach their offspring what is considered appropriate and inappropriate behaviour in the group. In humans, children learn what they are thought through imitation and internalization (Rakoczy et al. 2008; Tomasello et al. 1993) and human communication, with its ostensive signals, is argued to have an amplifying effect on social learning processes and enables them to be even more fast and effective (Cisbra and Gergely 2009). Since only enculturated chimpanzees are able to acquire rudimentary language systems (Rumbaugh et al. 2003; Savage-Rumbaugh et al. 1998)—using them predominantly in imperative rather than in declarative and informative modes—and since there is only very limited evidence for active teaching in chimpanzees (Boesch 1991), it is unlikely that any potential evolutionary precursor of a social norm in this species is transmitted via active teaching. It is important to note here that, provided that there is a strong genetic component underlying a social norm (or its precursor), i.e. it most likely is universal (see Table 1), active teaching and language are not necessarily required to acquire and maintain it. These capacities most likely only became so important in humans because we have to acquire from time of birth to adulthood relevant cultural knowledge, including a variety of often complex cultural social norms, to become socially accepted members of the cultural world (Cisbra and

Gergely 2009). Thus, the presence of an evolutionary precursor of a universal social norm in chimpanzees is not refuted by the near-absence of third-party punishment and active instructions on appropriate behaviour.

In conclusion, evidence available so far suggests that chimpanzees do not reach the level of collective social norms, i.e. norms to which all members of a group are committed and know together that they are committed because the absence of shared intentionality constrains them to do so. This is relevant, for it means that chimpanzees lack “truly intersubjective sharing” and hence the ability to create the aforementioned “common psychological ground” which would enable them to engage in collaborative activities with shared goals such as creating norm-maintaining social institutions (Tomasello and Carpenter 2007). No other animal species, except humans, create social institutions with accompanying social norms. Again, this exemplifies the collective and hence deeply social character of human social norms whether they are cultural or universal. However, from this does not follow that chimpanzees cannot form *social* expectations about the way in which others should be treated and react accordingly upon their violation. The challenge that we face now is how to measure these expectations. Assuming that the evolutionary transition from amoral to moral behaviour occurred gradually (Killen and de Waal 2000), chimpanzees might not only perform at the amoral end of this transition. Indeed, they might possess proto social norms.

Testing the theoretical framework

We have outlined the hypothesis that severe aggression against infants could constitute a norm violation in chimpanzees. In the following, we would like to propose experimental paradigms to test this hypothesis. For obvious ethical reasons, we cannot experimentally induce severe aggression against infants in a chimpanzee community to investigate the animals’ reactions towards such behaviour. Hamlin et al. (2007) successfully studied preverbal human infants’ expectations of others’ helping behaviour by measuring how long they looked at unknown individuals that either actively helped or hindered another unknown individual. This experiment was based on a violation of expectation paradigm that assessed infant’s *social* expectations via their looking duration, taking advantage of the fact that infants tend to look longer at unexpected events (Kuhlmeier et al. 2003; Wang et al. 2004; Woodward 1998). Interestingly, the same phenomenon is also known in nonhuman primates, and has been exploited to investigate their social (Bergman et al. 2003; Burkart 2004; Cheney and Seyfarth 1999; for chimpanzees see Slocombe et al. 2009) as well as physical knowledge (for chimpanzees see Cacchione and Krist 2004; Santos and Hauser 2002). We think that looking duration measurements can also be exploited to study the presence of evolutionary precursors of social norms and their underlying *social* expectations in chimpanzees. We therefore suggest to expose chimpanzees to different videos (of *unfamiliar* chimpanzees) with variable emotional charge, including scenes of lethal aggression towards *unfamiliar* infants (i.e. infanticide), and to monitor their respective looking durations as well as various behavioural and physiological reactions, both of which can be used as reliable

indicators of negative emotional arousal. Since nonhuman primates are *nonverbal* their possible *social* expectations have to be read from their behaviours and their possible emotional states from their behaviours as well as physiology. Otherwise, there is no possibility to inquire them at least not until some fundamentally different approach is developed.

Behavioural signs of negative emotional arousal include increased levels of yawning, of locomotory unrest (i.e. walking around) and of self-directed behaviour such as scratching (Aureli and van Schaik 1991; Troisi 2002). Correspondingly, aggressive behaviours directed at the television screen showing the videos also offer us valuable information about the animals' emotional state. Physiological signs of negative emotional arousal comprise decreased skin temperature and/or increased tympanic temperature (Parr 2001; Parr and Hopkins 2000) and are, as already mentioned earlier in this paper, known correlates of negative emotional arousal in humans. We predict two possible outcomes for the proposed experiments: (a) Chimpanzees look longer at videos including scenes of severe aggression against infants² and show higher levels of emotional arousal during such scenes or (b) chimpanzees show no specific reactions towards infanticidal scenes.

If we find (a) this would suggest the presence of at least a quasi social norm in chimpanzees. Additionally, if we can show that chimpanzees look longer at and react more strongly to scenes in which an infant is harmed by a conspecific compared to scenes in which an infant is merely harmed by a physical accident, then their reactions can be definitely ascribed to a perceived norm violation per se. A control condition of this kind is crucial when investigating a potential sensitivity towards harm-related violations in chimpanzees: for both events can potentially elicit distinct reactions in bystanders. However, only the former event elicits indignation in bystanders whereas the latter elicits compassion. Accordingly, preschool children consider events involving (moral) harm caused by others (pushing a child off the swing) as more wrong than harm caused by the self (a child jumping off the swing and getting hurt)—even when the consequences of harm caused by the self are depicted as more severe (Tisak 1993). Interestingly, in humans, each of these contexts appear to activate different regions in the brain (Moll et al. 2005). Furthermore, if we can also exclude the possibility that the increased looking durations and emotional arousal during infanticide are not caused by alternative stimuli such as for example the presence of infants, frantic movement, screaming and the presence of unfamiliar males, then this would lend strong support to the presence of a proto social norm in chimpanzees.

However, if we find (b) there are two possibilities to consider: either (i) chimpanzees do not perceive severe aggression against infants as a norm violation and thus have no *social* expectations about the appropriate treatment of infants, or (ii) social norms might only be deployed towards group members and therefore chimpanzees ignore the mistreatment of *unfamiliar* infants by *unfamiliar* conspecifics. Social norms are thought to emerge through within-group social interactions

² To eliminate the possibility that the animals' longer looking durations for videos including severe aggression against infants do not merely express surprise, the animals under investigation should be familiar with such incidents. Furthermore, the content of the different videos is to be chosen such that surprise can be excluded as an alternative explanation for the animals' looking behaviour.

(Ellikson 2001), and hence are likely to apply only to in-group members (Bowles and Gintis 2004). Since chimpanzees exhibit high within-group solidarity together with high out-group hostility (Boesch 2009), the mistreatment of *unfamiliar* infants might indeed have no effect on other chimpanzees. However, if a social norm is universal such in-group versus out-group distinctions are not expected or at least to become less pronounced. Consequently, bystanders are expected to be sensitive to harm-related violations that concern out-group members as well. On the contrary, violations of cultural social norms are expected to provoke strong reactions only in bystanders who share the cultural social norms of the victim, but not in those who do not share them.

To distinguish between (i) and (ii) one could conduct follow-up experiments with videos that would depict scenes of severe aggression against infants from their own group. Such incidents need not be induced experimentally since they occur naturally, yet rarely. If chimpanzees still do not react, this would strongly suggest the absence of any expectations concerning the appropriate behaviour towards infants. However, if chimpanzees clearly react towards severe aggression against *unfamiliar* infants per se, despite being *completely uninvolved* bystanders, this would underscore that chimpanzees indeed might form strong *social* expectations about the adequate behaviour towards infants, suggesting the presence of a proto social norm in this species. Thus, if chimpanzees differentially evaluate social events as “disinterested” bystanders then this can be regarded as a necessary foundation of any developing moral system. If this were to be found, chimpanzees would fulfil a crucial component of genuine moral behaviour.

Conclusion

Chimpanzees possess many parallels with humans in the cognitive as well as in the behavioural domain. Like humans, chimpanzees exhibit a community life in which individuals repeatedly interact with each other on a long-term basis and in which harmony and stability plays a central role. We therefore think that chimpanzees are an excellent species in which to study evolutionary precursors of human social norms. In this paper, we focused on those related to harm and aimed at exploring their evolutionary precursors in chimpanzees.

Social norms entail the existence of *social* expectations. Consequently, individuals not only form expectations about how they themselves would like to be treated, i.e. *personal* expectations, but most importantly also about how others should to be treated, i.e. *social* expectations. There is ample evidence showing that chimpanzees possess expectations about the behaviour of others towards themselves. They, thus, minimally possess what we term “personal norms”. However, do they, like humans, also form *social* expectations? In humans, behavioural patterns that do not fulfil these expectations almost always ensue negative reactions, not only in the victim, but also in *uninvolved* bystanders. Negative reactions from such “disinterested” bystanders can be regarded as pertaining to the realm of moral behaviour. One way to test possible candidates of evolutionary precursors of social norms in chimpanzees and the *social* expectations that might underlie them is to

assume the existence of a certain *social* expectation and then to violate it. Based on the fact that chimpanzee infants enjoy almost unlimited tolerance and hence seem to occupy a special status within their groups, we have proposed that tolerance towards infants could constitute a possible universal social norm in chimpanzees, and argued that severe aggression against them might violate chimpanzees' *social* expectation about how to treat infants. We also proposed a preliminary theoretical framework to decide whether the extreme tolerance, which is afforded to chimpanzee infants, constitutes only a *statistical* behavioural regularity or whether it constitutes an evolutionary precursor of a norm, *as such*. Finally, we proposed experimental paradigms to test this. As discussed, a fully-fledged moral system including collective social norms and abstract principles of right and wrong is beyond the capacities of chimpanzees. However, if chimpanzees differentially evaluate social events as "disinterested" bystanders then this can be regarded as an important step from amoral towards moral behaviour, especially in social contexts related to harm.

Although this paper focused exclusively on chimpanzees, other animals (e.g. social canids, elephants), whose natural history resembles that of humans in various aspects (division of labour, systematic food-sharing, shared care of young and impaired individuals), should also be considered when discussing the evolution of moral behaviour (Bekoff 2001, 2004). Thus, the question whether chimpanzees or "any animal whatever, endowed with well-marked social instincts" as Darwin (1871/1982) put it, form *social* expectations about how others, especially infants, should be treated has great potential, and gives us important insights into the presence of specific social norms in humans and furthermore is highly relevant for the understanding of the evolution of moral behaviour.

Acknowledgments This research was conducted at the Anthropological Institute & Museum of the University of Zurich and funded by the University Priority Research Program in Ethics of the University of Zurich. We thank the two anonymous reviewers for their valuable comments and Johannes Fischer for his help on an earlier draft of this paper.

References

- Abarbanell L, Hauser MD (2010) Mayan morality: an exploration of permissible harms. *Cognition* 115:207–224
- Alley TR (1980) Infantile coloration as an elicitor of caretaking behaviour in old world primates. *Primates* 21(3):416–429
- Anderson JR, Myowa-Yamakoshi M, Matsuzawa T (2004) Contagious yawning in chimpanzees. *Proc R Soc Lond B* 271:468–470
- Aureli F, van Schaik C (1991) Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II. Coping with uncertainty. *Ethology* 89:101–114
- Axelrod R (1986) An evolutionary approach to norms. *Am Polit Sci Rev* 80(4):1095–1111
- Baker KC, Smuts BB (1994) Social relationships of female chimpanzees: diversity between captive social groups. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) *Chimpanzee cultures*. Harvard University Press, Cambridge, pp 227–242
- Bauer RM (1998) Physiologic measures of emotion. *J Clin Neurophysiol* 15:388–396
- Bekoff M (2001) Social play behaviour: cooperation, fairness, trust, and the evolution of morality. *J Consc Stud* 8(2):81–90
- Bekoff M (2004) Wild justice and fair play: cooperation, forgiveness, and morality in animals. *Biol Philos* 19:489–520

- Bennett H (1996) Study of kinship, social relations and possible incest among Budongo chimpanzees. Master Thesis, Edinburgh University
- Beran MJ, Evans AT (2006) Maintenance of delay of gratification by four chimpanzees (*Pan troglodytes*): the effect of delayed reward visibility, experimenter presence, and extended delay intervals. *Behav Processes* 73:315–324
- Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank and kinship in baboons. *Science* 302:1234–1236
- Bernard G (2008) The definition of morality. In: Zalta EN (ed) *The stanford encyclopedia of philosophy*. <http://plato.stanford.edu/archives/fall2008/entries/morality-definition/>. Accessed Fall 2010
- Bethea L (1999) Primary prevention of child abuse. *Am Fam Physician* 59:1577
- Bicchieri C (ed) (2006) *The grammar of society: the nature and dynamics of social norms*. Cambridge University Press, New York
- Bischof-Köhler D (1989) *Spiegelbild und Empathie—Die Anfänge der sozialen Kognition*. Hans Huber, Bern
- Blaffer Hrdy S (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13–40
- Blaffer Hrdy S (1999) *Mother nature: a history of mothers, infants, and natural selection*. Pantheon Books, New York
- Boehm C (1994) Pacifying interventions at Arnhem Zoo and Gombe. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) *Chimpanzee cultures*. Harvard University Press, Cambridge, pp 211–226
- Boesch C (1991) Teaching among wild chimpanzees. *Anim Behav* 41:530–532
- Boesch C (1994) Cooperative hunting in wild chimpanzees. *Anim Behav* 48(3):653–667
- Boesch C (2007) What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *J Comp Psychol* 121:227–240
- Boesch C (2009) *The real chimpanzee*. Cambridge University Press, Cambridge
- Boesch C, Boesch-Achermann H (2000) *The chimpanzees of the Tai forest: behavioral ecology and evolution*. Oxford University Press, Oxford
- Bonnie KE, Horner V, Whiten A, de Waal FBM (2007) Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proc R Soc Lond B* 274:367–372
- Bott E (2003) *Family and social network: roles, norms, and external relationships in ordinary urban families*. Routledge Chapman & Hall, London
- Bowles S, Gintis H (2004) Persistent parochialism: trust and exclusion in ethnic networks. *J Econ Behav Organ* 55:1–23
- Boyd R, Richerson PJ (1987) The evolution of ethnic markers. *Cult Anthropol* 2(1):65–79
- Brosnan SF (2006) Nonhuman species' reactions to inequity and their implications for fairness. *Soc Justice Res* 19(2):153–185
- Brosnan SF, Schiff HC, De Waal FBM (2005) Tolerance for inequity may increase with social closeness in chimpanzees. *Proc R Soc Lond B* 272:253–258
- Burkart JM (2004) *Evolutionäre Vorläufer der theory of mind. Experimente zur sozialen Kognition bei Weissbüschelaffen (Callithrix jacchus)*. Dissertation, University of Zurich
- Cacchione T, Krist H (2004) Recognizing impossible object relations: intuitions about support in chimpanzees (*Pan troglodytes*). *J Comp Psychol* 118:140–148
- Call J (2007) Social knowledge in primates. In: Dunbar RIM, Barrett L (eds) *Handbook of evolutionary psychology*. Oxford University Press, New York, pp 71–81
- Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn Sci* 12:187–192
- Campbell MW, Carter JD, Proctor D, Eisenberg ML, de Waal FBM (2009) Computer animations stimulate contagious yawning in chimpanzees. *Proc R Soc Lond B* 276:4255–4259
- Castles DL, Whiten A (1998) Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. *Ethology* 104(2):148–160
- Cheney DL, Seyfarth RM (1990) Attending to behavior versus attending to knowledge: examining monkeys' attribution of mental states. *Anim Behav* 40:742–753
- Cheney DL, Seyfarth RM (1999) Recognition of other individuals' social relationships by female baboons. *Anim Behav* 58:67–75
- Christensen PN, Rothgerber H, Wood W, Matz DC (2004) Social norms and identity relevance: a motivational approach to normative behavior. *Pers Soc Psychol Bull* 30:1295–1309
- Cisbra G, Gergely G (2009) Natural pedagogy. *Trends Cogn Sci* 13(4):148–153

- Commons ML, Wolfson CA (2002) A complete theory of empathy must consider stage changes. *Behav Brain Sci* 25:30–31
- Cords M, Aureli F (2000) Reconciliation and relationship quality. In: Aureli F, de Waal FBM (eds) *Natural conflict resolution*. University of California Press, London, pp 177–199
- Cross G (2004) *The cute and the cool: wondrous innocence and modern american children's culture*. Oxford University Press, Oxford
- Daly M, Wilson M (1988) Evolutionary social psychology and family homicide. *Science* 242:519–524
- Darwin C (1982) *The descent of man, and selection in relation to sex*. Princeton University Press, Princeton
- de Waal FBM (1982) Chimpanzee politics: power and sex among apes. Unwin Paperbacks, London
- de Waal FBM (1984) Sex differences in the formation of coalitions among chimpanzees. *Ethol Sociobiol* 5(4):239–255
- de Waal FBM (1989) Dominance 'style' and primate social organization. In: Standen V, Foley RA (eds) *Comparative socioecology: the behavioural ecology of humans and other mammals*. Blackwell Scientific Publications, London, pp 243–263
- de Waal FBM (1991) The chimpanzee's sense of social regularity and its relation to the human sense of justice. *Am Behav Sci* 34(3):335–349
- de Waal FBM (1996) *Good natured: the origins of right and wrong in humans and other animals*. Harvard University Press, Cambridge
- de Waal FBM (2000) Primates—a natural heritage of conflict resolution. *Science* 289:586–590
- de Waal FBM (2005) *Our inner ape*. Riverhead Books, New York
- de Waal FBM (2008) Putting the altruism back into altruism: the evolution of empathy. *Annu Rev Psychol* 59(1):279–300
- de Waal FBM, Hoekstra JA (1980) Contexts and predictability of aggression in chimpanzees. *Anim Behav* 28(3):929–937
- de Waal FBM, van Hooff JARAM (1981) Side-directed communication and agonistic interactions in chimpanzees. *Behaviour* 77(3):164–198
- de Waal FBM, van Roosmalen A (1979) Reconciliation and consolation among chimpanzees. *Behav Ecol Sociobiol* 5(1):55–66
- Denant-Boemont L, Masclet D, Noussair C (2007) Punishment, counterpunishment and sanction enforcement in a social dilemma experiment. *Econ Theory* 33:145–167
- Dufour V, Pelé M, Sterck EHM, Thierry B (2007) Chimpanzees (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. *J Comp Psychol* 121(2):145–155
- Efferson C, Lalive R, Richerson PJ, McElreath R, Lubell M (2008) Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evol Hum Behav* 29:56–64
- Ellikson RC (2001) The evolution of social norms: a perspective from the legal academy. In: Hechter M, Opp KD (eds) *Social norms*. Russell Sage Foundation, New York, pp 35–75
- Elster J (1989) *The cement of society—a study of social order*. Cambridge University Press, Cambridge
- Fehr E, Fischbacher U (2002) Social norms and human cooperation. *Trends Cogn Sci* 8(4):185–190
- Fehr E, Fischbacher U (2004) Third-party punishment and social norms. *Evol Hum Behav* 25:63–87
- Fehr E, Gächter S (2002) Altruistic punishment in humans. *Nature* 415:137–140
- Finch G (1943) The bodily strength of chimpanzees. *J Mammal* 24(2):224–228
- Flack JC, de Waal FBM (2002) Any animal whatever: darwinian building blocks of morality in monkeys and apes. In: Katz LD (ed) *Evolutionary origins of morality: cross-disciplinary perspectives*. Imprint Academic, Thorverton, pp 1–29
- Flack JC, Jeannotte LA, de Waal FBM (2004) Play signaling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *J Comp Psychol* 118(2):149–159
- Flack JC, de Waal FBM, Krakauer DC (2005) Social structure, robustness, and policing cost in a cognitively sophisticated species. *Am Nat* 165(5):E126–E139
- Flack JC, Girvan M, de Waal FBM, Krakauer DC (2006) Policing stabilizes constructions of social niches in primates. *Nature* 439:426–429
- Frank SA (2003) Perspective: repression of competition and the evolution of cooperation. *Evolution* 57(4):693–705
- Fraser ON, Aureli F (2008) Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. *Am J Primatol* 70:1114–1123
- Fraser ON, Stahl D, Aureli F (2008) Stress reduction through consolation in chimpanzees. *PNAS* 105(25):8557–8562

- Fuentes A (1999) Variable social organization: what can looking at primate groups tell us about the evolution of plasticity in primate societies? In: Dolhinow P, Fuentes A (eds) *The nonhuman primates*. Mayfield Publishing Company, London, pp 183–188
- Gallup GGJ (1970) Chimpanzees: self-recognition. *Science* 167:241–243
- Gallup GGJ (1979) Self-recognition in chimpanzees and man: a developmental and comparative perspective. Plenum Press, New York
- Gilbert R, Spatz Widom C, Browne K, Fergusson D, Webb E, Janson S (2009) Burden and consequences of child maltreatment in high-income countries. *Lancet* 373:68–81
- Glazko GV, Nei M (2003) Estimation of divergence times for major lineages of primate species. *Mol Biol Evol* 20(3):424–434
- Goodall J (1971) *In the shadow of man*. Houghton Mifflin, Boston
- Goodall J (1977) Infant killing and cannibalism in free-living chimpanzees. *Folia Primatol* 28:259–282
- Goodall J (1986) *The chimpanzees of Gombe: patterns of behavior*. The Belknap Press of Harvard University, Cambridge
- Goodall J, Bandora A, Bergmann E, Busse C, Matama H, Mpongo E, Pierge A, Riss D (1979) Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: Hamburg DA, McCown ER (eds) *The great apes*. Benjamin/Cummings, California, pp 13–53
- Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP (1998) Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Mol Phylogenet Evol* 9(3):585–598
- Greene J, Haidt J (2002) How (and where) does moral judgment work? *Trends Cogn Sci* 6(12):517–523
- Hall KRL (1964) Aggression in monkey and ape societies. In: Carthy JD, Ebling FJ (eds) *The natural history of aggression*. Academic Press, London, pp 51–64
- Hamai M, Nishida T, Takasaki H, Turner LA (1992) New records of within-group infanticide and cannibalism in wild chimpanzees. *Primates* 33(2):151–162
- Hamlin JK, Wynn K, Bloom P (2007) Social evaluation by preverbal infants. *Nature* 450:557–559
- Hatters Friedman S, Resnick PJ (2007) Child murder by mothers: pattern and prevention. *World Psychiatry* 6:137–141
- Hauser MD (2006) *Moral minds: how nature designed our universal sense of right and wrong*. HarperCollins Publishers, New York
- Hayaki H (1985) Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* 26(4):343–360
- Hechter M, Opp KD (2001) *Social norms*. The Russell Sage Foundation, New York
- Heim C, Nemeroff CB (2001) The role of childhood trauma in the neurobiology of mood and anxiety disorders: preclinical and clinical studies. *Biol Psychiatry* 49:1023–1039
- Hess J (1997) *Menschenaffen mütter und kind*. Friedrich Reinhardt Verlag, Basel
- Hill K (2009) Animal “culture”? In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, pp 269–287
- Hill K, Barton M, Hurtado M (2009) The emergence of human uniqueness: characters underlying behavioral modernity. *Evol Anthropol* 18(5):187–200
- Hiraiwa-Hasegawa M, Hasegawa T (1994) Infanticide in nonhuman primates: sexual selection and local resource competition. In: Parmigiani S, vom Saal FS (eds) *Infanticide & parental care*. Harwood Academic Publisher, Singapore, pp 137–155
- Hirata S, Celli ML (2003) Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Anim Cogn* 6:235–244
- Hoffman ML (1979) Development of moral thought, feeling, and behavior. *Am Psychol* 34(10):958–966
- Hoffman ML (2000) *Empathy and Moral Development: Implications for Caring and Justice*. Cambridge University Press, Cambridge
- Horne C (2001) Sociological perspectives on the emergence on norms. In: Hechter M, Opp KD (eds) *Social norms*. The Russell Sage Foundation, New York, pp 3–34
- Hrdy SB (2005) Evolutionary context of human development: the cooperative breeding model. In: Carter CS, Ahnert L, Grossmann KE et al (eds) *Attachment and bonding: a new synthesis; from the 92nd Dahlem workshop report*. MIT Press, Cambridge, pp 9–32
- Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J Comp Psychol* 111(2):159–173
- Janssen MA, Bushman C (2008) Evolution of cooperation and altruistic punishment when retaliation is possible. *J Theor Biol* 254:541–545

- Jasso G (2001) Rule finding about rule making: comparison processes and the making of rules. In: Hechter M, Opp KD (eds) *Social Norms*. Russell Sage Foundation, New York, pp 348–394
- Jeannotte LA (1996) Play-signaling in juvenile chimpanzees in relationship to play intensity and social environment. Emory University, Atlanta
- Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc R Soc Lond B* 273:1013–1021
- Jensen K, Call J, Tomasello M (2007) Chimpanzees are vengeful but not spiteful. *PNAS* 104(32):13046–13050
- Kanazawa S, Still MC (2001) The emergence of marriage norms: an evolutionary psychological perspective. In: Hechter M, Opp KD (eds) *Social norms*. Russell Sage Foundation, New York, pp 274–305
- Kawanaka K (1981) Infanticide and cannibalism in chimpanzees, with special reference to the newly observed case in Mahale Mountains. *Afr Study Monogr* 1:69–99
- Khagram S, Riker JV, Sikkink K (2002) Restructuring world politics: transnational social movements, networks, and norms. University of Minnesota Press, Minneapolis
- Killen M, de Waal FBM (2000) The evolution and development of morality. In: Aureli F, de Waal FBM (eds) *Natural conflict resolution*. University of California Press, London, pp 352–372
- Killen M, McGlothlin H, Lee-Kim J (2002) Between individuals and culture: individuals' evaluations of exclusion from social groups. In: Keller H, Poortinga Y, Schoelmerich A (eds) *Between biology and culture: perspectives on ontogenetic development*. Cambridge University Press, Cambridge, pp 159–191
- Kitchen A, Denton D, Brent L (1996) Self-recognition and abstraction in the common chimpanzee studied with distorting mirrors. *PNAS* 93:7405–7408
- Köhler W (1925) *The mentality of apes*. Kegan Paul, Trench, Trubner & Co., London
- Koski SE, Sterck EHM (2007) Triadic postconflict affiliation in captive chimpanzees: does consolation console? *Anim Behav* 73:133–142
- Koski SE, Sterck EHM (2009a) Empathetic chimpanzees: a proposal of the levels of emotional and cognitive processing in chimpanzee empathy. *Eur J Dev Psychol* 7(1):38–66
- Koski SE, Sterck EHM (2009b) Post-conflict third-party affiliation in chimpanzees: what's in it for the third party? *Am J Primatol* 71:1–10
- Koski SE, de Vries H, van den Tweel SW, Sterck EHM (2007) What to do after a fight? The determinants and inter-dependency of post-conflict interactions in chimpanzees. *Behaviour* 144:529–555
- Kuhlmeier V, Wynn K, Bloom P (2003) Attribution of dispositional states by 12-month-olds. *Psychol Sci* 14(5):402–408
- Lehmann HE (1979) Yawning: a homeostatic reflex and its psychological significance. *Bull Menninger Clin* 43:123–136
- Leigh SR, Shea BT (1995) Ontogeny and the evolution of adult body size dimorphism in apes. *Am J Primatol* 36:37–60
- Lorenz K (1943) Die angeborenen Formen möglicher Erfahrung. *Z Tierpsychol* 5(2):235–409
- Marlowe FW (2009) Hadza cooperation: second-party punishment, yes; third-party punishment, no. *Hum Nat* 20:417–430
- Marlowe FW, Berbesque JC, Barr A, Barrett C, Bolyanatz A, Cardenas JC, Ensminger J, Gurven M, Gwako E, Henrich J, Henrich N, Lesorogol C, McElreath R, Tracer D (2008) More “altruistic” punishment in larger societies. *Proc R Soc Lond B* 275:587–590
- Marsh B (2002) Do animals use heuristics? *J Bioecon* 4:49–56
- Mendoza-Granados D, Sommer V (1995) Play in chimpanzees of the Arnhem Zoo: self-serving compromises. *Primates* 36(1):57–68
- Mitani JC (2009) Cooperation and competition in chimpanzees: current understanding and future challenges. *Evol Anthropol* 18(5):215–227
- Moghadam VM (2003) *Modernizing women: gender and social change in the middle east*. Lynne Rienner, Boulder
- Moll J, Zahn R, de Oliveira-Souza R, Krueger F, Grafman J (2005) The neural basis of human moral cognition. *Nat Neurosci* 6:799–809
- Muller MN (2002) Agonistic relations among Kanyawara chimpanzees. In: Boesch C, Hohmann G, Marchant LF (eds) *Behavioural diversity in chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp 112–124
- Murdock GP (1967) *Ethnographic atlas*. University of Pittsburgh Press, Pittsburgh

- Murray CM, Wroblewski E, Pusey AE (2007) New case of intragroup infanticide in the chimpanzees of Gombe national park. *Int J Primatol* 28(1):23–37
- Newton-Fisher NE (2006) Female coalitions against male aggression in wild chimpanzees of the Budongo forest. *Int J Primatol* 27(6):1589–1599
- Nichols S (2002) Norms with feeling: towards a psychological account of moral judgment. *Cognition* 84:221–236
- Nichols S (2004) Sentimental rules. Oxford University Press, New York
- Nishida T (1983) Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* 24(3):318–336
- Nishida T, Hosaka K (1996) Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew W, Marchant L, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 114–135
- Nishida T, Kawanaka K (1985) Within-group cannibalism by adult male chimpanzees. *Primates* 26:274–284
- Norikoshi K (1982) One observed case of cannibalism among wild chimpanzees of the Mahale Mountains. *Primates* 23:66–74
- Nucci LP (2001) Education in the moral domain. Cambridge University Press, Cambridge
- Nucci LP, Turiel E (1978) Social interactions and the development of social concepts in preschool children. *Child Dev* 49:400–407
- Osvath M, Osvath H (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim Cogn* 11:661–674
- Parr LA (2001) Cognitive and physiological markers of emotional awareness. *Anim Cogn* 4:223–229
- Parr LA, Hopkins WD (2000) Brain temperature asymmetries and emotional perception in chimpanzees, *Pan troglodytes*. *Physiol Behav* 71:363–371
- Penn DC, Povinelli DJ (2007) On the lack of evidence that non-human animals possess anything remotely resembling a ‘theory of mind’. *Philos Trans R Soc B* 362:731–744
- Platek SM, Critton SR, Myers TE, Gallup GG Jr (2003) Contagious yawning: the role of self-awareness and mental state attribution. *Cogn Brain Res* 17:223–227
- Platteau JP (2000) Institutions, social norms, and economic development (fundamentals of development economics). Harwood Academic Publishers, Singapore
- Potegal M (2000) Post-tantrum affiliation with parents: the ontogeny of reconciliation. In: Aureli F, de Waal FBM (eds) Natural conflict resolution. University of California Press, London, pp 253–255
- Povinelli D, Vonk J (2003) Chimpanzee minds: suspiciously human? *Trends Cogn Sci* 7:157–160
- Povinelli DJ, Parks KA, Novak MA (1991) Do rhesus monkeys (*Macaca mulatta*) attribute knowledge and ignorance to others? *J Comp Psychol* 105:318–325
- Preston S, de Waal FBM (2002) Empathy: its ultimate and proximate bases. *Behav Brain Sci* 25:1–72
- Pusey A, Williams J, Goodall J (1997) The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277(5327):828–831
- Pusey AE, Oehlert GW, Williams JM, Goodall J (2005) Influence of ecological and social factors on body mass of wild chimpanzees. *Int J Primatol* 26(1):3–31
- Rakoczy H, Warneken F, Tomasello M (2008) The sources of normativity: young children’s awareness of the normative structure of games. *Dev Psychol* 44(3):878–881
- Reynolds V (2005) The chimpanzees of the Budongo forest: ecology, behaviour, and conservation. Oxford University Press, New York
- Richerson PJ, Boyd R (2005) Not by genes alone: how culture transformed human evolution. Chicago University Press, Chicago
- Rosati AG, Stevens JR, Hare B, Hauser MD (2007) The evolutionary origins of human patience: temporal preferences in chimpanzees, Bonobos, and human adults. *Curr Biol* 17:1663–1668
- Rumbaugh DM, Beran MJ, Savage-Rumbaugh ES (2003) Language. In: Maestripietri D (ed) Primate psychology. Harvard University Press, London, pp 395–423
- Ruvolo M (1997) Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol Biol Evol* 14(3):248–265
- Sakamaki T, Itoh N, Nishida T (2001) An attempted within-group infanticide in wild chimpanzees. *Primates* 42(4):359–366
- Santos L, Hauser MD (2002) A non-human primate’s understanding of solidity: dissociations between seeing and acting. *Dev Sci* 5(2):F1–F7
- Savage-Rumbaugh S, Shanker SG, Taylor JT (1998) Apes, language, and the human mind. Oxford University Press, New York

- Schino G, Geminiani S, Rosati L, Aureli F (2004) Behavioral and emotional response of Japanese macaque (*Macaca fuscata*) mothers after their offspring receive an aggression. *J Comp Psychol* 118(3):340–346
- Scott ES (2000) Social norms and the legal regulation of marriage. *Va Law Rev* 86(8):1901–1970
- Silk J (2000) The function of peaceful post-conflict interactions: an alternative view. In: Aureli F, de Waal FBM (eds) *Natural conflict resolution*. University of California Press, London
- Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli D, Richardson AS, Lambeth SP, Mascaro J, Schapiro SJ (2005) Chimpanzees are indifferent in the welfare of unrelated group members. *Nature* 437:1357–1359
- Slocombe KE, Townsend SW, Zuberbühler K (2009) Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: evidence from a playback study. *Anim Cogn* 12:441–449
- Smetana JG (1981) Preschool children's conceptions of moral and social rules. *Child Dev* 52:1333–1336
- Smetana JG (2006) Social domain theory: consistencies and variations in children's moral and social judgments. In: Killen M, Smetana JG (eds) *Handbook of moral development*. Lawrence Erlbaum Associates, Mahwah, pp 119–154
- Smetana JG, Braeges JL (1990) The development of toddlers' moral and conventional judgments. *Merrill Palmer Q* 36:329–346
- Sober E, Wilson DS (1998) *Unto others—the evolution and psychology of unselfish behavior*. Harvard University Press, Cambridge
- Sommer V (2000) The holy wars about infanticide. Which side are you on? and why? In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 9–26
- Takahata Y (1985) Adult male chimpanzee kill and eat a male newborn infant: newly observed intragroup infanticide and cannibalism in Mahale Mountains National Park, Tanzania. *Folia Primatol* 44:161–170
- Tisak M (1993) Preschool children's judgments of moral and personal events involving physical harm and property damage. *Merrill Palmer Q* 39:375–390
- Tomasello M (1999) *The cultural origins of human cognition*. University Press, Cambridge
- Tomasello M, Call J (1997) *Primate cognition*. Oxford University Press, New York
- Tomasello M, Carpenter M (2007) Shared intentionality. *Dev Sci* 10(1):121–125
- Tomasello M, Kruger AC, Ratner HH (1993) Cultural learning. *Behav Brain Sci* 16:495–552
- Tomasello M, Carpenter M, Call J, Behne T, Moll H (2005) Understanding and sharing intentions: the origins of cultural cognition. *Behav Brain Sci* 28:675–735
- Townsend SW (2007) Female-led infanticide in wild chimpanzees. *Curr Biol* 17(10):R355–R356
- Troisi A (2002) Displacement activities as a behavioral measure of stress in nonhuman primates and human subjects. *Stress* 5(1):47–54
- Turiel E (1983) *The development of social knowledge: morality & convention*. Cambridge University Press, Cambridge
- Turiel E (2005) Thought, emotions, and social interactional processes in moral development. In: Killen M, Smetana JG (eds) *Handbook of moral development*. Lawrence Erlbaum Associates, Mahwah, pp 7–36
- van Lawick-Goodall J (1968) The behaviour of free-living chimpanzees in the Gombe Stream area. *Anim Behav Monogr* 1:161–311
- van Schaik CP (2000) Infanticide by male primates: the sexual selection hypothesis revisited. In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 27–61
- van Schaik CP (2003) Local traditions in orangutans and chimpanzees: social learning and social tolerance. In: Frigaszy DM, Perry S (eds) *The biology of traditions: models and evidence*. Cambridge University Press, Cambridge, pp 297–329
- van Schaik CP, Pradhan GR, van Noordwijk MA (2004) Mating conflict in primates: infanticide, sexual harassment and female sexuality. In: Kappeler P, van Schaik CP (eds) *Sexual selection in primates: new and comparative perspectives*. Cambridge University Press, Cambridge, pp 131–150
- Vetlesen AJ (1994) Perception, empathy, and judgment: an inquiry into the preconditions of moral performance. The Pennsylvania State University Press, University Park
- Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ, Povinelli DJ (2008) Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Anim Behav* 75:1757–1770

- Wang SH, Baillargeon R, Brueckner L (2004) Young infants' reasoning about hidden objects: evidence from violation-of-expectation tasks with test trials only. *Cognition* 93(3):167–198
- Warneken F, Tomasello M (2006) Altruistic helping in human infants and young chimpanzees. *Science* 311(5765):1301–1303
- Warneken F, Hare B, Melis AP, Hanus D, Tomasello M (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biol* 5(7):e184
- Whiten A (1998) Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 112(3):270–281
- Whiten A (2005) The second inheritance system of chimpanzees and humans. *Nature* 437:52–55
- Whiten A (2010) Ape behavior and the origins of human culture. In: Kappeler PM, Silk JB (eds) *Mind the gap: tracing the origins of human universals*. Springer, Berlin, pp 429–451
- Whiten A, Cusance DM, Gomez JC, Teixidor P, Bard KA (1996) Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J Comp Psychol* 110(1):3–14
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CE, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682–685
- Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:737–740
- Wiessner P (2009) Experimental games of life among the Ju/'hoan Bushmen. *Curr Anthropol* 50(1):133–138
- Williams J, Liu AY, Pusey AE (2002) Costs and benefits of grouping for female chimpanzees at Gombe. In: Boesch C, Hohmann G, Marchant LF (eds) *Behavioural diversity in chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp 192–203
- Wittling W (1995) Brain asymmetry in the control of autonomic physiologic activity. In: Davidson RJ, Hugdahl K (eds) *Brain asymmetry*. MIT Press, Cambridge, pp 305–357
- Woodward AL (1998) Infants selectively encode the goal object of an actor's reach. *Cognition* 69:1–34
- Wrangham RW (1999) Evolution of coalitionary killing. *Am J Phys Anthropol* 110(S29):1–30
- Wrangham RW, de Waal FBM, McGrew WC (1994) The challenge of behavioural diversity. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) *Chimpanzee cultures*. Chicago Academy of Sciences, Chicago, pp 1–21
- Yamamoto S, Tanaka M (2010) The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. *Anim Behav* 79:595–602
- Yamamoto S, Humle T, Tanaka M (2009) Chimpanzees help each other upon request. *PloS One* 4(10):e7416
- Young HP (2002) The power of norms. In: Hammerstein P (ed) *Genetic and cultural evolution of cooperation*. The MIT Press, Cambridge, pp 389–399
- Young HP (2008) Social norms. *The new Palgrave dictionary of economics*. Macmillan, London
- Zahn-Waxler C, Radke-Yarrow M, Wagner E, Chapman M (1992) Development of concerns for others. *Dev Psychol* 28:126–136